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Growth, gas exchange, and root respiration of *Quercus rubra* seedlings exposed to low root zone temperatures in solution culture

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Abstract

Spring planting is standard operational practice in the Central Hardwood Region, though little is known about potential impacts of low root temperature (RT) common during spring on establishment success of temperate deciduous forest tree species. The effects of low RT on growth, gas exchange, and root respiration following winter dormancy were studied in 1-year-old northern red oak (*Quercus rubra* L.) container seedlings grown in solution culture at uniform air temperatures, but exposed to three different root zone temperatures (10, 15, and 25 °C). After 14 days of treatment, net photosynthesis (A), stomatal conductance (g_s), and transpiration (E) were significantly affected by RT; however, these treatment effects did not persist for the remaining measurement period (days 21 and 28) despite growth reductions. After 28 days, new shoot length, leaf area, and number of new roots were reduced with decreasing RT. Shoot dry mass was higher in seedlings exposed to 25 °C compared with those in 10 °C, while an opposite trend occurred for root-to-shoot ratio. Leaf water potential (ψ_w) at day 28 and days to budbreak were not significantly altered by RT treatments. Root O_2 uptake in seedlings exposed to 10 °C was 65% lower than for those seedlings at 25 °C. Low RT has a physiological role in the control of root growth and root respiration, which could potentially affect establishment success of northern red oak seedlings planted in spring when soil temperatures are still low.

Keywords: Hardwood seedlings; Northern red oak; Root growth; Root physiology; Transplanting stress

1. Introduction

Field establishment success of newly planted seedlings is largely dictated by the environmental factors to which they are exposed to at the time of planting. The ability of seedlings to produce new roots shortly after transplanting is critical to regeneration success (Grossnickle, 2005), as these new roots facilitate water and nutrient uptake (Häusling et al., 1988; Jacobs et al., 2004a). Low soil temperature has been shown to inhibit root growth of newly planted conifer seedlings (Lopushinsky and Kaufmann, 1984; Amponsah et al., 2004). Although much research has been conducted on the effects of low root zone temperatures on seedling growth and physiology in conifers (Delucia, 1986; Grossnickle, 1988; Ryyppö et al., 1998; Amponsah et al., 2004), little is known about this phenomenon in temperate deciduous forest tree species. To our knowledge, there are no recent studies conducted on the effects of low root zone temperature with northern red oak (*Quercus rubra* L.) and oaks in general. Most studies conducted with oak species were restricted to examining shoot and root growth (Larson, 1970, 1971; Teskey and Hinckley, 1981) and therefore the transient physiological mechanisms by which low root temperatures inhibit seedling growth in northern red oak are not well understood.

In the Central Hardwood Region of the USA, temperate deciduous forest tree species such as northern red oak are usually planted in early spring (Pijut, 2004; Seifert et al., 2006) during late February to early April when root zone temperatures at planting sites are below favorable levels for root growth. At Wooster, Ohio, USA, for example, soil temperature at planting

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depth averages less than 12 °C during April and does not reach 20 °C until mid-June (Pierce et al., 1966). This temperature range could potentially affect root system proliferation (Larson, 1970; Tryon and Chapin, 1983) and in turn, growth and seedling establishment success. Farmer (1975) found that slow root growth delays the establishment of northern red oak transplants. Soil temperatures ranging from 24 to 29 °C were ideal for northern red oak (Larson, 1971) and white oak (*Q. alba* L.) (Larson, 1974). In addition, there are reports of reduced root growth at temperatures below 17 °C in white oak (Teskey and Hinckley, 1981) and at 13 °C in northern red oak (Larson, 1970, 1971).

Northern red oak exhibits episodic growth in which shoot growth occurs as distinct flushes, controlled by endogenous factors, within a growing season (Dickson, 1994). Seedlings grown under favorable conditions (i.e., moisture, light, and temperature) showed repeated flushes of shoot growth (Hanson et al., 1986). However, root zone temperature effects on budbreak, patterns of shoot flushing, and leaf developmental stages of northern red oak have not yet been thoroughly examined. It is likely that reduction in root proliferation associated with low RT could inhibit root O_2 uptake, which could also alter leaf flushing and expansion. Because northern red oak seedlings store a large proportion of carbohydrates in roots during dormancy (Farmer, 1975), it is possible that low RT affects budbreak by influencing carbohydrate mobilization.

Seedlings planted in cold soils have also shown reduced growth (Landhäusser and Lieffers, 1998; Amponsah et al., 2004) and photosynthesis (Folk et al., 1995). Many critical root functions are dependent upon energy supplied through root respiration. Low RT inhibits root respiration and results in reduced nutrient uptake and root growth (Martinez et al., 2002). Similarly, low soil temperature can also reduce plant water uptake as a result of decreased root permeability and increased water viscosity (Kaufmann, 1975), thereby potentially affecting growth, gas exchange, and survival following transplanting.

Spring planting when soil temperature is low may have substantial impacts on transplanting success of northern red oak seedlings. Grossnickle (1988) indicated that trees may be more susceptible to low RT-induced water stress shortly after planting, and physiological stresses may be expressed within 28 days (Larson, 1970; Wan et al., 1999). Although spring planting is standard operational practice in the Central Hardwood Region, little is known about potential impacts of low RT on transplanting success of temperate deciduous forest tree species. Understanding the effects of soil temperature on seedling growth is critical for identifying ideal seasonal time frames for outplanting. Thus, we examined mechanisms by which low RT affects growth and physiology of transplanted northern red oak, a primary species used for conservation tree plantings in the Central Hardwood Region (Jacobs et al., 2004b). We tested the hypothesis that low RT inhibits root growth, leaf water potential (ψ_w), and root O_2 uptake leading to lower assimilation rates, which in turn, may inhibit seedling growth. Our objective was to build on the work of Seifert et al. (2006) regarding the ideal timing of planting of temperate deciduous forest tree species and potential for root growth under varying soil temperature regimes.

2. Materials and methods

2.1. Plant material and treatments

Northern red oak acorns, collected from a single open-pollinated tree adjacent to the Purdue University campus, West Lafayette, IN, USA (40°25′N, 86°55′W), were germinated and seedlings grown for 18 weeks in 2.8-l Treepot™ containers (Stuewe and Sons, Corvallis, OR, USA) filled with Scotts Metro-Mix® 560 growing medium (The Scotts Company, Marysville, OH, USA). The medium is comprised of 35–54% composted pine bark, 20–30% processed coconut coir pith, 10–20% sphagnum peat moss, 5–15% processed bark ash, and 5–15% horticultural perlite. Seedlings received a seasonal dose rate of 50 mg N plant^{-1}, applied exponentially as previously described (Salifu and Jacobs, 2006). Seedlings were grown in a greenhouse at the Department of Horticulture and Landscape Architecture Plant Growth Facility at Purdue University, West Lafayette IN, USA (40°25′N, 86°55′W). The greenhouse was set to day/night air temperatures of 24/20 °C, relative humidity of 60–70% and 16-h photoperiods with photosynthetic photon flux density (PPFD), measured at seedling top height of 400 μmol m^{-2} s^{-1}. Lights were provided by a combination of 400-W metal halide and high-pressure sodium lamps.

After 18 weeks in the greenhouse, seedlings were moved into a lath house for hardening under ambient conditions for 3 months, and then transferred to freezer storage at −2 °C for about 6 months prior to initiation of the current experiment. The frozen, dormant seedlings, with mean (±S.E.) height of 19.4 ± 1.4 cm, were thawed at 25 °C overnight. After the roots had been washed free of soil, seedlings were randomly divided into three groups and transferred to insulated tanks (45 cm × 45 cm × 30 cm, $L \times W \times D$) (Aqua Logic, Inc., San Diego, CA, USA) filled with aerated mineral nutrient solution from a 200 mg l^{-1} 15N–5P_2O_5–15K_2O water soluble fertilizer (Miracle-Gro® Excel® Cal-Mag; The Scotts Company, Marysville, OH, USA) in three replicated containers at temperatures of 10, 15, and 25 °C. The two lower temperatures were chosen to mimic typical soil temperatures that occur during spring planting in the Central Hardwood Region, while the 25 °C temperature provided near optimum temperature for root growth (Larson, 1971). The nutrient solution contained (in mg l^{-1}) 150 N, 22 P, 125 K, 50 Ca, 20 Mg, and micronutrients. The design of the study was a randomized complete block design.

The desired temperature of the nutrient solution was maintained using thermoelectric coolers (Model TC-24-25 RS232, TE Technology, Inc., MI, USA) connected to circulating pumps (EW-07105-00, March MFG, Inc., Glenview, IL, USA). The dissolved O_2 concentrations, which were measured using an oxygen electrode YSI Model 58 (Yellow Springs Instruments, Yellow Spring, OH, USA), were in the range of 10–12 mg l^{-1}. The nutrient solution was changed every week and the solution levels were maintained as needed with addition of deionized water. Deionized water was added to bring the nutrient solution to the original volume but did not maintain the aforementioned nutrient concentrations.

After initiation of RT treatments, seedlings were grown in a growth room under the following environmental conditions: day/night air temperature, 24/18 °C; relative humidity, 65%; 16-h photoperiod with PPFD of 450 μmol m^{-2} s^{-1} measured at seedling top height. Light was provided by metal halide and high-pressure sodium lamps (800 W Dual Spectrum Plant Grow Light, Specialty-Lights.com, Ronkonkoma, NY, USA).

2.2. Measurements

Gas exchange measurements (net photosynthesis, A; stomatal conductance, g_s; transpiration, E) were conducted 3–5 h after photoperiod initiation using a LI-6400 portable infrared gas analyzer equipped with a red LED light source (LI6400-02) and a CO_2 mixer control unit (LI-COR, Lincoln, NE, USA). Measurements were taken on the second leaf from the top of the first flush on six different seedlings from each treatment on days 14, 21, and 28 after initiation of RT treatments. All measurements were made at PPDF of 450 μmol m^{-2} s^{-1}, reference CO_2 concentration of 400 μmol m^{-2} s^{-1}, leaf temperature of 24 °C, RH of 55–60%, and flow rate at 500 μmol s^{-1}. Following enclosure in the leaf cuvette, data was logged when a leaf reached a steady-state value (coefficient of variations of CO_2 and H_2O within the chamber was <0.25%).

A SPAD-502 chlorophyll meter (Minolta, Ramsey, NJ, USA) was used, as per Markwell et al. (1995), to acquire a rapid and non-destructive estimate of leaf chlorophyll content. Measurements were taken on the uppermost attached, fully expanded leaf halfway from the leaf base to the tip and halfway from the midrib to the leaf margin.

Midday leaf water potential (ψ_w) was measured with a Scholander pressure chamber (PMS Instruments, Corvallis, OR, USA). Root respiration was measured as oxygen uptake using an oxygen electrode, YSI Model 58 (Yellow Springs Instruments, Yellow Spring). The oxygen probe and intact roots were placed in a 1.5 l airtight cylinder filled with aerated nutrient solution at 10 and 25 °C that was continuously stirred with a magnetic stirrer. The root respiration cylinder was placed in a temperature-controlled water bath set at the desired 10 and 25 °C. Due to difficulty in maintaining the small temperature fluctuation of the two lower temperatures (i.e., 10 and 15 °C) in the root respiration cylinder and time constrains, we only measured root respiration for the low (10 °C) and high (25 °C) temperatures. Root respiration was monitored for 20 min by recording oxygen uptake every 4 min. Root respiration rates were calculated as a mean of oxygen uptake over time and values were expressed in mmol O_2 g^{-1} root fresh weight (FW) min^{-1}. Both leaf water potential and root O_2 uptake were measured at the final measurement period. Number of new roots and root respiration were only obtained from seedlings exposed to 10 and 25 °C at the end of the experimental period. Days to budbreak were recorded whenever the terminal bud scales parted to expose new (green) foliage. Leaf area was determined with an LI-6200 leaf area meter (LI-COR, Lincoln, NE, USA) and tissue dry mass was obtained after oven drying at 70 °C for 72 h.

2.3. Data analysis

Tests for normality and constant variance were performed to ensure validity of the assumptions of analysis of variance (ANOVA) and no transformations were necessary. Data were analyzed with SAS (SAS Institute Inc., Cary, NC) using only a general linear model because the results of an earlier analysis of covariance (ANCOVA), which tested the effects of initial shoot height (covariate), were insignificant for measured variables. When ANOVA indicated significant ($P < 0.05$) RT effects, Tukey's Studentized Range Test was used to identify significant differences among RT treatments at $\alpha = 0.05$. Gas exchange variables were analyzed for each measurement period. The data presented reflects the means of six seedlings from each RT treatment ($n = 6$).

3. Results

By the end of the treatment period (day 28), RT treatment did not significantly affect days to budbreak ($P = 0.3060$) (data not shown). In general, however, we observed that seedlings exposed to 15 and 25 °C flushed twice compared to a single flush for those exposed to 10 °C. Although seedlings exposed to 15 °C flushed twice, flushing was delayed and leaves did not fully expand by the end of the experiment. Mean length of new shoots was significantly affected by RT ($P = 0.0020$) (Fig. 1A). Seedlings exposed to 10 and 15 °C had a 74 and 42% reduction in mean new shoot length, respectively, compared with those in the 25 °C RT treatment. Total leaf area in the 25 °C treatment was 855 cm^2, compared with 427 and 254 cm^2 for those seedlings exposed to 15 and 10 °C, respectively ($P = 0.0012$) (Fig. 1B). After 28 days, chlorophyll index was not significantly ($P = 0.1145$) affected by RT treatments (data not shown).

Shoot and root dry mass were affected by RT (Fig. 2) ($P = 0.004$). Root dry mass was greater than shoot dry mass at both 10 and 15 °C, while shoot and root dry mass were similar to those seedlings exposed to 25 °C. Shoot dry mass was significantly reduced (35%) in seedlings in the 10 °C treatment compared with 25 °C. Root-to-shoot ratio was significantly ($P = 0.0248$) greater in seedlings exposed to 10 °C compared with 25 °C. Root-to-shoot ratio in seedlings exposed to 10 °C was 1.21 compared with 0.51 in the 25 °C treatment. The shoot and root dry mass and root-to-shoot ratio in seedlings exposed to 15 °C were not significantly different from the 10 and 25 °C RT treatments.

After 14 days of treatment, A ($P = 0.0232$), g_s ($P = 0.0002$), and E ($P = 0.0007$) were significantly affected by RT (Fig. 3). Seedlings exposed to 25 °C had the highest A, g_s, and E values followed next by those in 15 °C and then by seedlings in 10 °C. For instance, mean A values for seedlings in 25 °C were 2.24 μmol CO_2 m^{-2} s^{-1} followed by 1.69 and 1.11 μmol CO^2 m^{-2} s^{-1} in the 15 and 10 °C temperature treatments, respectively. RT treatment effects, however, on A, g_s, and E were non-significant after 21 and 28 days of treatment exposure.

RT did not significantly ($P = 0.3350$) affect ψ_w of northern red oak after 28 days of treatment (data not shown). Root O_2

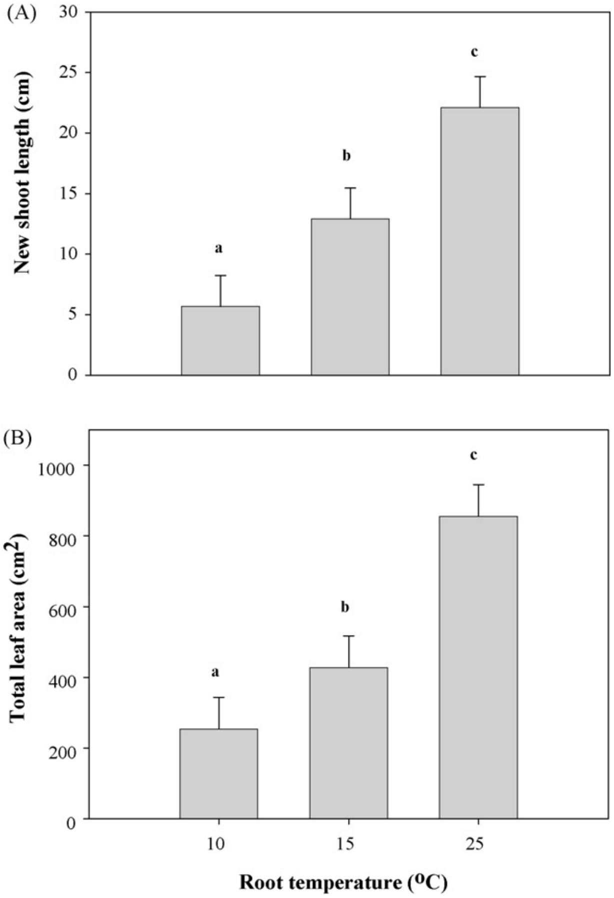

Fig. 1. (A) New shoot length and (B) total leaf area of *Quercus rubra* seedlings grown at root temperatures of 10, 15, and 25 °C for 28 days. Least square means ± S.E. ($n = 6$) are shown. Bars with different letters indicate significant differences as determined by Tukey's Studentized Range Test at $\alpha = 0.05$.

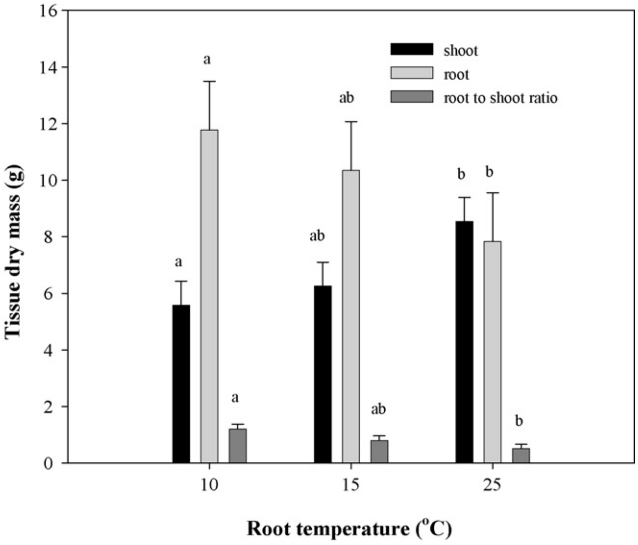

Fig. 2. Tissue dry mass and root-to-shoot ratio of *Quercus rubra* seedlings grown at root temperatures of 10, 15, and 25 °C for 28 days. Least square means ± S.E. ($n = 6$) are shown. For each response parameter, bars with different letters are significantly different as determined by Tukey's Studentized Range Test at $\alpha = 0.05$.

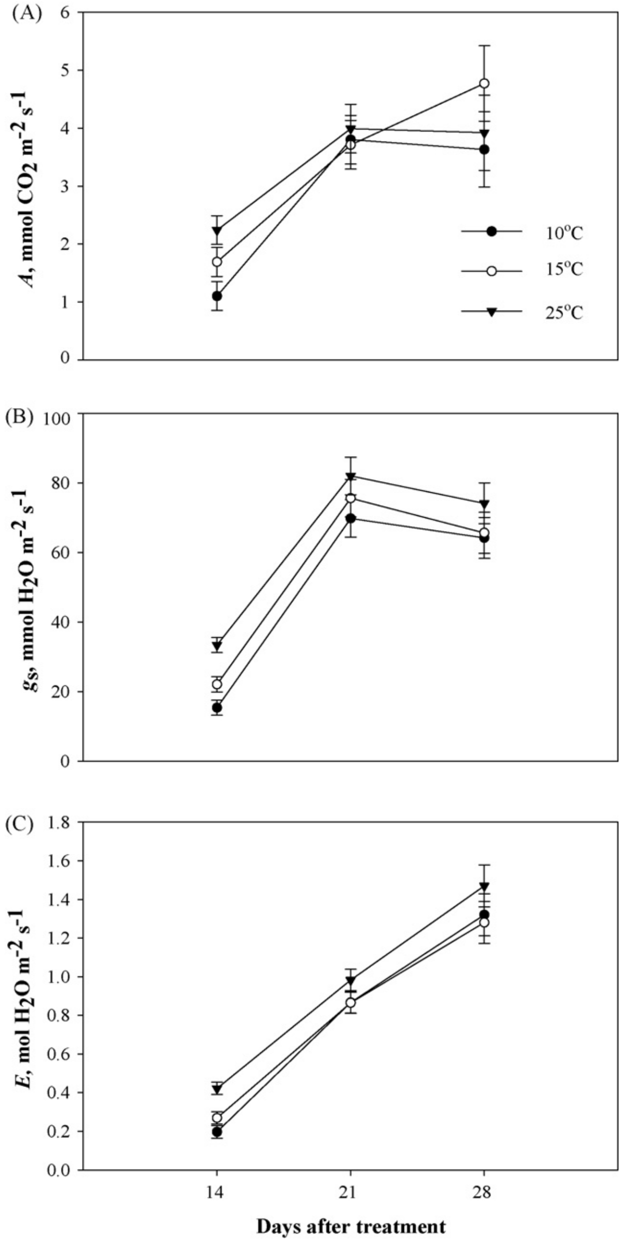

Fig. 3. (A) Net photosynthesis, *A*; (B) stomatal conductance, g_s; (C) transpiration, *E*, in *Quercus rubra* seedlings grown at root temperatures of 10, 15, and 25 °C for 28 days. Each data point represents least square means ± S.E. ($n = 6$).

uptake ($P = 0.0314$) and number of new roots ≥ 5 cm ($P = 0.0003$) were significantly reduced at low RT (Fig. 4). Root O_2 uptake and number of new roots for seedlings exposed to 10 °C were 65 and 86%, respectively, lower than for those at 25 °C. We observed that seedlings grown at 10 °C had thick and stunted roots, while roots grown at 25 °C were longer and had numerous lateral roots.

4. Discussion

After 28 days of treatment, shoot dry mass was significantly reduced with decreasing RT treatments (Fig. 2); however, an opposite RT effect was observed for root dry mass. Low RT effects on root growth were different

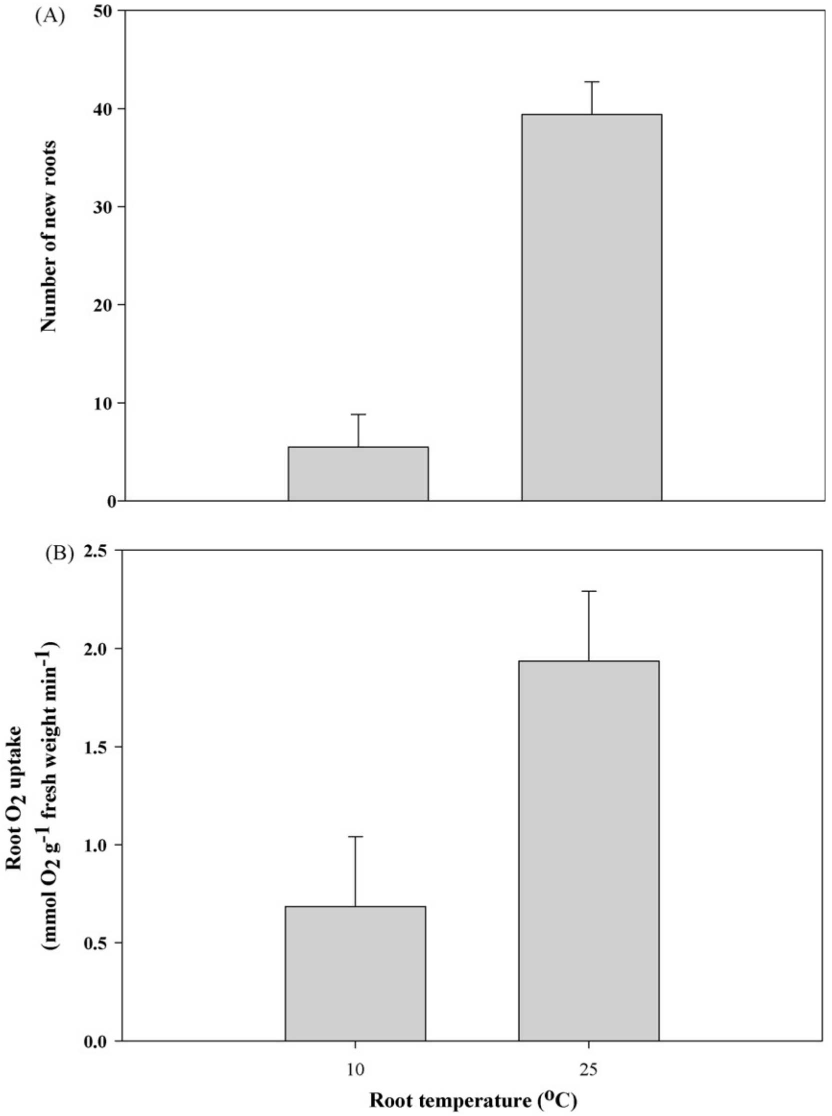

Fig. 4. (A) Root oxygen uptake and (B) number of new roots of *Quercus rubra* seedlings grown at root temperatures of 10, 15, and 25 °C for 28 days. Least square means ± S.E. (n = 6) are shown. For each response parameter, treatment means were significantly different as determined by Tukey's Studentized Range Test at $\alpha = 0.05$.

when expressed in terms of root dry mass (Fig. 2) and number of new roots (Fig. 4A). Root dry mass decreased with increasing temperature while an opposite trend was observed for number of new roots. The reduced root dry mass with increasing RT treatments in spite of significant reductions in new shoot length and total leaf area suggests that roots may respond differently to low RT than shoots. Regarding the opposite RT effects on shoots and roots observed in the present study, we speculate that red oak seedlings responded to low RT through internal redistribution of stored carbon in the roots as a response to stress. While greater root dry mass was noted at 10 °C, we observed reductions in new shoot length, leaf area, and root respiration (Figs. 1 and 4), suggesting that greater root dry mass at low temperature did not appear to provide a protective role for low root temperature stress. Similar to our results, low RT inhibited shoot, leaf, and new root growth of several forest tree species (Landhäusser and Lieffers, 1998; Folk et al., 1995; Amponsah et al., 2004). Contrary to our results, previous authors did not observe an increase in root dry mass with decreasing root temperature. However, similar to our studies, number of new roots was reduced with decreasing soil temperature (Fig. 4A).

Leaf water potential is known to be influenced by low RT (Wan et al., 1999; O'Hare, 2004). However, midday ψ_w was statistically insignificant in all RT treatments at the end of 28 days. Plant water relations are a variable process dependent on diurnal circumstances (Else et al., 1995; Clarkson et al., 2000). Because seedlings grown at 25 °C had larger leaf area than those at lower temperatures, we speculate that they may have been rapidly transpiring at photoperiod onset but by midday may have experienced an upset in water relations (which may have also restricted gas exchange) that coincided with timing of measurements. This may partly explain lack of significant differences among root temperature treatments. Additionally, influence of hormonal signals, which originate in roots, on stomatal behavior cannot be discounted.

Wan et al. (1999) reported significant reductions in gas exchange variables and growth reductions at the end of a 28-day treatment exposure to low RT. We found significant differences in gas exchange 14 days after treatment, but no statistical evidence of differences in gas exchange variables by the end of 28 days (Fig. 3). Although we did not observe significant RT treatment effects on time to budbreak (first flush), differences in leaf developmental stages were noticeable on the second flush with leaf expansion and maturity being delayed in those seedlings grown at the lowest RT. Photosynthetic capacity increases as leaves develop, becoming maximal at or around full expansion and subsequently declining at full maturation (Kozlowski et al., 1991). Vogelmann et al. (1982) showed that young leaves are typically strong sinks for photosynthates while mature leaves are strong sources. In the present study, leaf developmental stages (i.e., maturity) were altered by low RT after 21 days. Thus, it is possible that the effect of RT on leaf developmental stages along with corresponding variation in diurnal tendencies for transpiration and stomatal closure may have masked the RT effects on gas exchange parameters and ψ_w during the phenological period represented by the current study. Hanson et al. (1986) observed that net photosynthesis in red oak increased with leaf development stage during a flush and decreased from one flush to the next. Thus, influence of low RT on gas exchange and plant water relations may be more important as a longer-term effect and cannot explain the physiological responses reported in the shorter-term duration of the present study. Additionally, longer treatment duration could have produced greater significant treatment effects on gas exchange and episodic growth flushes between plants exposed to warm compared to cold RT.

We observed that budbreak occurred prior to the emergence of new roots (data not shown). This finding has been noted by other studies where root growth occurred shortly after budbreak in newly planted northern red oak (Johnson et al., 1984; Crow, 1988; Struve and Joly, 1992). Such response may further aggravate transplanting success. We found that seedlings exposed to 10 °C had fewer new roots compared with those grown at 25 °C (Fig. 4A), suggesting that low RT may have exacerbated transplanting problems in northern red oak as similarly observed for lodgepole pine (*Pinus contorta* Dougl. ex. Loud.) seedlings (Amponsah et al., 2004). Although we did not monitor emergence of new roots for all RT treatments, new root emergence was first observed in seedlings at 25 °C after 11 days of treatment exposure. We propose that an increased number of new roots was likely related to greater production of photosynthates, with leaves acting as a source of metabolites for the roots (sink) as demonstrated by larger leaf area in seedlings exposed to 25 °C (855 cm^2) compared to those grown at 10 °C (254 cm^2) or 15 °C (427 cm^2). Sustained addition of new leaves in seedlings at warmer media temperature could increase net assimilation rates that in turn, may result in much greater seedling biomass accumulation.

Our study showed that low temperatures in the range and time (midday) measured did not significantly affect ψ_w and impact on E and A was limited only to day 14. Although root temperature effects on gas exchange and ψ_w failed to demonstrate instantaneous effects at the time of measurements, our study clearly suggests that irrespective of leaf physiological mechanisms, RT influences seedling growth through effects on new root growth and root metabolic activity. The alterations of overall growth and root oxygen uptake were a result of the cumulative effect of low RT, which was an integration of other physiological processes not reported in the present study. Carbohydrate mobilization may be one factor involved (Taiz and Zeigler, 2002) but evidence also exists of chemical signaling at low RT (Atkin et al., 1973; Tahtiharju et al., 2001), which may play a role in growth inhibition.

Root growth generally declines with decreasing RT in the 5–30 °C range, and reduced whole-plant growth and photosynthetic rate may be a result of less water and nutrient uptake at low RT (Bowen, 1991). It has been reported that decline in root hydraulic conductivity due to low RT is linked to limitations in new root growth (Wan et al., 1999). Fewer new roots produced at 10 °C may have caused reduction in root water flow, which in turn, reduced seedling growth. In our study, the lower number of new roots observed at 10 °C may suggest reduced numbers of functional roots available for water transport. While greater root dry mass was observed at 10 °C, we observed presence of older, suberized roots and root mortality that may have caused poor water uptake and impaired root metabolic activity. Newly regenerated roots have been found to be more efficient at water uptake than older (suberized) roots (Sands et al., 1982). Another factor involved in seedling growth inhibition due to low RT is decreased root metabolic activity (Kramer and Boyer, 1995). This may partly explain the lower root respiration rates observed in those seedlings exposed to 10 °C compared with those grown at 25 °C (Fig. 4B). Generally, root respiration increased with increasing root temperature, typical of many metabolic processes (Atwell et al., 1999), which is consistent with our findings. Kamaluddin and Zwiazek (2002) showed that a decline in root water flow due to reduced water channel activity was reflected by a decline in root respiration. The lack of new roots due to low root zone temperature may be linked to reduced root respiration. Although not determined here due to the larger volume of the whole root system, it is widely accepted that low RT inhibits water conductance properties (Bowen, 1991; Wan et al., 1999).

Although we did not measure tissue nutrient (particularly N) levels, we did not observe differences in chlorophyll index among RT treatments. Nitrogen deficiency is known to result in chlorophyll reduction; therefore, absence of chlorophyll reductions observed in the present study suggests that low RT may not affect short-term nutritional status at least in respect to N.

5. Conclusions

We have shown that low RT inhibited root respiration, growth of new and functional roots, new shoot length, and total leaf area. However, RT did not alter chlorophyll index, which suggests RT had no apparent effect on pigment content and foliar nutrient status. Although ψ_w was not altered by the temperatures in the range and time (midday) measured and gas exchange parameters were only affected at day 14, longer-term growth effects are possible due to influences of RT on root physiology as demonstrated by a decline in root respiration and new root growth. These factors may significantly affect transplanting success of northern red oak seedlings planted in spring when temperature is below levels optimum for root growth. Interest in transplanting outside the traditional spring planting season (Good and Corell, 1982; Seifert et al., 2006) suggests that additional research is needed to further examine the interrelationship between seedling dormancy development (over-wintered versus non-acclimated seedlings), root growth potential, and site environmental conditions to help optimize transplanting success.

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